

A NESTING OF THE CAROLINA WREN

BY MARGARET M. NICE AND RUTH H. THOMAS¹

THE Carolina Wren, *Thryothorus ludovicianus*, charming, conspicuous, and widely distributed as it is throughout southeastern United States, has been much neglected by life-history students. And this in spite of the fact that it often leaves its characteristic woods habitat to nest about buildings and even on porches. In 1946 we were able to watch one nesting of this species from the arrival of the female to the leaving of the young.

The male, which had been banded March 27, 1941, near North Little Rock, Arkansas, had lost a mate in late March 1946. On April 18 we noted him bringing three wisps of grass and placing them under the eaves of the sleeping porch. (Typically, in Ruth Thomas' experience, a male does not build until mated.) On April 19 we first saw his new mate, an unbanded bird.

BUILDING THE NEST

In the afternoon of April 19, the new female came onto the porch, then flew to the base of a nearby oak; the male suddenly dropped down from his perch, hitting her and giving a loud song; she answered with the typical "screech" of the female Carolina. Later we discovered them nest-hunting in a shed to the south; we removed the grape baskets that were stored there and hung one (partially closed with a shingle) on the sleeping porch.

The next morning (April 20), at 7:55, both came to the porch; they entered the basket, gave little notes, then left. For a while both carried material into the tool-shed, some 25 yards to the east. At 8:25 the female returned to the basket and gave little notes, while her mate sang nearby. At 8:32 she brought the first load of material and gave notes in the basket; at 8:33 the male entered and left again; the female came with material, and he followed with a load. She had carried 5 loads and he 6 when, at 8:38, they were frightened away by a boy coming to the porch. They then made a number of trips with leaves, and the male tried to insert a large twig but dropped it; at 9:11 they left. We scattered dead leaves and other nesting material in front of the porch and placed lichen and cat's fur from the nest of a Carolina Chickadee, *Parus carolinensis*, on a nearby chair.

At 11:50 the male brought material, gave "nest notes" in the basket, and sang loudly. Four minutes later, both were investigating under the eaves. The male then went to the basket without a load, and his

¹ Although the study as a whole was cooperative and largely based on R. H. T.'s previous experience with the Carolina Wren gained through many years of intensive banding, observation, and recording, M.M.N. is responsible for the larger part of the observations recorded here (covering the period April 16-May 28, 1946) and, in the main, for the writing of the paper.

mate carried a dead leaf in and out again. He then drove off a male Bewick's Wren, *Thryomanes bewickii*, with a *scat* note and sang loudly. We saw nothing more of them that day until 3:15, when the male made two trips to the basket with empty bill. While inside, he uttered tiny squeaks; his mate did not appear. We did not know whether they had finally selected the basket for their nest.

At 6:50 a.m. on April 21 the male came to the basket without a load, entered, gave nest notes, then sang once from the edge; his mate joined him; both entered and stayed for about 3 minutes. Then he brought two loads. At 7 o'clock she carried in a large load and gave many notes inside—*fit fit fit fit*; he joined her, bringing nothing, left, and returned twice with loads. She came with dead grass, but went onto the roof. He then brought 8 loads of moss and bits of cypress bark from the lawn chair; she gathered some grass but dropped it. The male carried 3 more loads, and at 7:17 she brought more material. By 7:20 he had brought 18 loads, she 4.

Both birds continued working, and between 8 and 10 o'clock the major part of the nest was constructed. The male carried 107 loads and his mate 54—a total of 161 loads—in the first hour; he carried 98 and she 50—a total of 148—in the second hour, making an average during the 2 hours of 1.7 trips per minute for the male and 0.9 trips a minute for his mate. The dead leaves, oak catkins, dry grass, and the few twigs that made up the nest were all gathered in the immediate vicinity—on the ground or from the roof. The female often chattered when she met her mate and often twittered in the basket. Once the male was scratching around in the nest and singing inside the basket; afterward he sang loudly 3 times on the ivy-covered oak, 10 feet from the nest; his mate came out from the ivy leaves; he sang again, then brought more loads and gave 2 songs in the nest. Whenever a Blue Jay, *Cyanocitta cristata*, appeared, he stopped work and *churred*—the note he used when one of the dogs stood on the porch beneath the basket.

Building zeal began to lessen, especially in the male. From 10:38 to 11:08 he brought 23 loads, she 18; from 12:20 to 12:35 he brought 2, she 5; from 1:23 to 1:38 he carried 4, she 8; and from 2:30 to 3:30 he made 3 visits, bringing a load on only one; and she 13, bringing material all but once. Little more happened that day until between 6:00 and 6:15 p.m., when he made 2 visits, bringing nothing, and she made 6 trips with material.

Although we were watching for "courtship displays," we saw little. At 12 noon the female gave a long trilling cry on the oak branch; the male went to her, and they may have copulated; he then sang, his feathers fluffed. Twice in the afternoon we saw him displaying before her with outspread wings, uttering a kind of *chur*, but she made no response. At 6:15, as they were foraging on the ground, he gave her a caterpillar, which she accepted without any demonstration. (On March

28, 1937, Mrs. Thomas saw a male Carolina Wren offering a caterpillar to his mate; the birds at that time were either building or about to build.)

The nest was practically completed during this great burst of energy the morning of April 21; the male's nest-building urge was satisfied, but that of the female did not entirely disappear until May 6, the eighth day of incubation.

On April 22 the pair arrived at 5:30 a.m., the female going into the basket, the male going onto the top. In the next hour and a half she came 15 times, bringing hair and fine grass. He visited the nest 3 times, sang a good deal, and displayed to her once on the wood-pile, but she gave no response. During the rest of the morning they paid a few visits to the basket, he empty-billed, she with more lining material; each gave soft notes at times in the basket.

The next morning (April 23) they arrived at 5:26 and gave little notes in the nest; in an hour and a half she carried in 14 bits of lining, while he made 3 more visits. From 7:45 to 8:45 she carried 2 loads and was very vocal in the nest. At 9:05 she was nowhere to be seen, and apparently the male was seeking her. After vigorous singing from the lawn chair and nearest oak branches, he went into the basket, gave a tiny note, and came out. He repeated this twice, the last time staying in for 2 minutes; then he sang loudly from the nearest oak and from other perches. One visit from the female early in the afternoon was our only other record for the day.

On April 24, after a heavy downpour late in the night, the Wrens did not arrive until 7:09 a.m.; the male went into the basket, while his mate scolded for 2 minutes with her bill full of dry grass; later they both entered. At 8:07, she brought a tiny root, and at 8:16 a few more small roots. These were the only visits during a continuous watch of over 5 hours.

EGG LAYING

On April 25, 6 days after her arrival and 5 days after the start of nest-building, the female laid her first egg. The times of her early morning departures and arrivals for the 5 days of egg-laying are given in Table 1.

From April 26 to 29 the female's absences from the nest showed a striking regularity, ranging between 23 and 26 minutes. When laying, she stayed on the nest from 30 to 64 minutes at a time; the two shortest periods and also the next to the longest were terminated by her departure in response to her mate's singing nearby. She arrived at the nest to lay her first egg some 9 minutes earlier in the day than on the following days. (In Finland, at latitude 63° N., in early June, with sunrise at about 2:30 a.m., one Willow-Warbler, *Phylloscopus trochilus*, went on the nest to lay at about 3:00 a.m. and another at 4:00 a.m., both going on the nest slightly earlier from day to day—Kuusisto,

TABLE 1
CAROLINA WREN, NORTH LITTLE ROCK, ARKANSAS
EGG LAYING

| 1946 April | Sky | Sunrise | Left nest | Came to lay | Minutes off | Left again | Minutes on |
|---------------|--------|---------|--------------|----------------|----------------|---------------|---------------|
| 25 | Clear | 5:26 | | 5:43 | | 6:24 | 41 |
| 26 | Clear | 5:25 | 5:33 | 5:56 | 23 | 6:30* | 30 |
| 27 | Clear | 5:23 | 5:28* | 5:54 | 26 | 6:25* | 31 |
| 28 | Clear | 5:22 | 5:29 | 5:54 | 25 | 6:58 | 64 |
| 29 | Cloudy | 5:21 | 5:26 | 5:51 | 24 | 6:47* | 56 |
| Average | | 5:23 | 5:29 | 5:52 | 24.5 | 6:37 | 44 |

* Apparently left in response to male's signal song.

1941:34.) On April 25 the Carolina Wrens came to the nest at 5:43 a.m.; the female entered the basket and gave loud chatterings inside; the male flew to the edge and looked down, whereupon his mate redoubled her notes. The night of April 25 was the first she spent in the basket.

Except for April 28, when we left for the day at 10:25, one of us was on the porch much of the time every day; on April 25 the female brought material 3 times during the morning after laying her egg and stayed from one to 28 minutes; on April 26 she did not reappear after 6:30 a.m., and on April 27 she made but one visit. The male came to the basket 2 or 3 times each morning; twice, on April 26 and April 28, he brought caterpillars; one he ate himself, since his mate was not at home. His first visit on April 28 was very early—5:18 a.m.; he looked down into the basket and gave 2 small notes, but getting no response he left; 11 minutes later his mate hopped onto the edge of the basket and flew off.

INCUBATION

During the 14 days of incubation we watched the nest from 2 to 14 hours a day. Unfortunately, owing to the amazingly long periods spent by the female on the nest and her quietness in leaving, as well as to our reluctance to disturb her by examining the nest basket, some data, especially for periods on the nest, are lacking from our records. Six hours, for instance, on May 10 and 11 yielded only one complete record (for a period off the nest) but did give data on the male's feeding of his mate.

At least 7 times during the first 8 days of incubation (April 29-May 6) the female brought catkins or a few hairs on her return to the nest. About half of her departures were apparently in response to her mate's singing nearby; twice she followed him after he had fed her.

Several times he brought food when she was not there; once, when he offered her a morsel a minute after her return, she did not accept it. He was most intent on feeding her early in the morning. On May 7 and 8 his zeal increased but waned in the next 3 days, only to increase again on the morning of the fourteenth (last) day of incubation, when he made 13 trips in 5 hours 30 minutes before the hatching of the first egg (about 1:43 p.m.).

Feeding of female by male during incubation was reported in the Carolina Wren by Wight (1934), but Laskey recorded none during the two nestings that she observed in July and August (1946b:62; and 1948). Laskey suggests that feeding may occur during early nestings only, as with the Cardinal, *Richmondena cardinalis* (Laskey, 1944:42). "Courtship feeding" seems never to have been reported for the Winter—or European—Wren, *Troglodytes troglodytes*, or for the House Wren, *Troglodytes aëdon*, both thoroughly studied species; nor for the marsh wrens, *Telmatodytes* and *Cistothorus* (Welter, 1935; Walkinshaw, 1935); but it does occur to some extent in the Rufous-browed Wren, *Troglodytes rufociliatus* (Skutch, 1940:308), Bewick's Wren (Miller, 1941:96; Laskey, 1946a:40), and Northern Cactus Wren, *Campylorhynchus brunneicapillus couesi* (Anders Anderson, letter).

The results of 92 hours of watching are summarized in Table 2. We obtained two all-day records as follows: May 2, the fourth day of incubation, dawned clear; the male gave his first song at 4:40 and came to the nest with food at 5:20; 8 minutes later the female left. His second offering, brought at 6:00, he ate himself, for the female had not returned. His third and last visit came at 5:13 p.m. The female's periods off and on the nest lasted the following numbers of minutes (periods off being in parentheses): (39), 45, (61), 147, (38), 119, (58), 119, (61), 85, (22). The 6 periods off the nest averaged 46.5 minutes; the 5 periods on the nest, 103 minutes. That evening, which was rainy, the male went to roost at 6:26 p.m., the female went to the nest for the night at 6:42. The morning of May 7 was cloudy. The male gave his first song at 4:52 and sang 188 times during the first hour. His first visit to the nest occurred at 5:27, and his mate left at 5:35; he brought food 8 times between 6:00 and 12:33 and once more at 6:38. The female's periods away from and on the nest were as follows: (20), 68, (30), 129, (25), 112, (17), 174, (36), 99, (20), 53, (18). The 7 periods off the nest averaged 24 minutes; the 6 on the nest 106 minutes. Thus, though the periods on the nest were as long as those of May 2, the periods off the nest averaged little more than half as long; 62 per cent of the daylight hours were spent on the nest on May 2, and 79 per cent on May 7, with mean temperatures of 75° F. and 64° F., respectively, being on May 2, 8° above normal, on May 7, 4° below. On May 7, a clear evening, the female went to the nest for the night at 6:55 p.m.

The most striking feature of the female's behavior during incubation was the very long periods spent on and off the nest. We never knew the female to spend less than half an hour on the nest; one session lasted nearly 3 hours (174 minutes), and the average for the whole fortnight was 86 minutes. Periods off the nest averaged 31 minutes in length.

A marked lengthening of the periods on the nest appeared on the fourth day (May 2); during the first 3 days, 11 periods averaged 65.6 minutes; during the last 11 days, 25 periods averaged 95.2 minutes. Two or more periods on the nest were observed on 6 of the days between May 2 and May 12; the daily average for 5 of these days ranged from 103 to 108 minutes, while on the other day 3 periods averaged 95 minutes. Shortening of the periods off the nest was evident from the fifth day (May 3): 19 periods in the first 4 days averaged 39 minutes, 27 periods in the last 10 days averaged 25 minutes. This shortening was more marked from the sixth day of incubation (May 4) and coincided with a drop in temperature, the mean temperature of the first 5 days averaging 69° F. (3° above normal), of the last 9 days, 63.6° F. (4.6° below normal); 64.5 per cent of the time was spent on the nest during 40.5 hours of observation on the warmer days, 80 per cent during 51.5 hours of observation on the cool days.

Very long periods on and off the nest were also recorded by Laskey (1946:62; 1948:107) in her study of two Carolina Wrens in Nashville, Tennessee. She watched one nest July 10 and 11, 1946, for 6 hours and 14 minutes; the female incubated 43 per cent of the time, staying on the nest from 15 to 87 minutes and off the nest from 41 to more than 85 minutes; temperatures were high (up to 94° F.). She watched the other nest for 67 hours during incubation, from July 21 to August 2, 1946; temperatures were normal, averaging 78.6° F., and daily fluctuations were small, ranging from 3° above normal to 3° below; 63 per cent of the time was spent on the nest; 33 periods on the nest ranged from 12 to 137 minutes, averaging 57.9 minutes, and 43 periods off the nest ranged from 9 to 58.5 minutes, averaging 33.5 minutes. Thus periods off the nest averaged almost the same as those of our Carolina Wren in Arkansas, but periods on the nest averaged a third shorter; whereas on the average both birds stayed off the nest a half hour at a time, the periods on the nest averaged for the Tennessee female about an hour (57.9 minutes), for the Arkansas female, about an hour and a half (86.1 minutes). Due to the comparative uniformity of the weather during Laskey's second study, it was not possible (as it was in our Arkansas study) to trace a difference in rhythm correlated with temperature changes; also, in Laskey's study, the periods on and off the nest were about the same during the first 4 days as during the last 10.

Periods spent on and off the nest by these three Carolina Wrens are very much longer than those of most small passerines that have so

TABLE 2
CAROLINA WREN, NORTH LITTLE ROCK, ARKANSAS
INCUBATION

| Date (1946) | Hours watched | Feedings by male | Periods on the nest | | Periods off the nest | | Time on nest (%) | Temperature (mean) USWB |
|--------------|---------------|------------------|---------------------|-------------------|----------------------|------------------|------------------|-------------------------|
| | | | No. | Length (minutes) | No. | Length (minutes) | | |
| Apr. 29 | 7.5 | 4 | 4 | 31-102 (63) | 4 | 11-84 (43.5) | 59.1 | 66°F. (0) |
| 30 | 4 | 4 | 2 | 31-74 (52.5) | 3 | 13-43 (25.3) | 67.5 | 66° (0) |
| May 1 | 11 | 3 | 5 | 46-112 (73) | 6 | 22-74 (37.5) | 62 | 70° (+4°) |
| 2 | 14 | 3 | 5 | 45-147 (103) | 6 | 22-61 (46.5) | 62.4 | 75° (+8°) |
| 3 | 4 | 1 | 1 | 74 | 2 | 23-49 (36) | 70.5 | 70° (+3°) |
| 4 | 6 | 3 | 3 | 89-104 (95) | 3 | 23-28 (25.3) | 78.9 | 62° (-5°) |
| 5 | 2 | 1 | 1 | 56 | 2 | 26-31 (28.5) | 60° | 60° (-7°) |
| 6 | 4.5 | 3 | 2 | 75-134 (104.5) | 2 | 26-41 (33.5) | 76 | 71° (+3°) |
| 7 | 14 | 10 | 6 | 53-174 (106) | 7 | 17-36 (24) | 79.4 | 64° (-4°) |
| 8 | 3.5 | 12 | 2 | 86-145 (105) | 3 | 15-19 (17) | 81.9 | 62° (-6°) |
| 9 | 6 | 5 | 1 | 43 | 3 | 8-35 (23.7) | | 64° (-4°) |
| 10 | 3.5 | 2 | | | 1 | 19 | | 70° (+1°) |
| 11 | 2.5 | 5 | | | | | | 59° (-10°) |
| 12 | 9.5 | 37* | 4 | 43-145 (108) | 4 | 14-32 (25.5) | 81.1 | 60° (-9°) |
| Total | 92 | 93† | 36 | 31-174 (86.1) | 46 | 8-84 (31.2) | 73.4 | 65.6° |
| First 5 days | 40.5 | 15 | 17 | 31-147 (71.3) | 21 | 11-84 (39.3) | 64.5 | 69° (+3°) |
| Last 9 days | 51.5 | 78‡ | 19 | 43-174 (99.6) | 25 | 8-41 (24.4) | 80.3 | 63.6° (-3.8°) |

Mean lengths of periodson and off the nest and degrees of departure from normal temperature are given in parenthesis in the respective columns. Data for 2 all-day records (May 2 and 7) are given in boldface type.

* 13 times in 5.5 hours before hatching of the first young (1:43 p.m.).

† 69 times in 86 hours before hatching of the first young.

‡ 45 times in 50 hours before hatching of the first young.

far been studied. For 21 individuals, of 8 species, listed by Nice (1943: 221, Table XXIII), average periods on the nest ranged from 12 to 49 minutes, with a median of 29.8; average periods off the nest ranged from 5.7 to 16.5 minutes, with a median of 8.5. The Northern Cactus Wren also has short periods of attentiveness and inattentiveness (Anders Anderson, letter).² The number of times the incubating female leaves the nest each day varies among 11 species from 11 to 90, with a median of 21 (Nice, 1943:220). The Carolina Wren of this study left the nest 6 and 7 times (on the 2 days of complete records). The House Wren leaves 27 to 43 times a day (Baldwin and Kendeigh, 1927:213). The Oven-bird, *Seiurus aurocapillus*, seems to be the only passerine so far studied with an incubation rhythm at all comparable with that of the Carolina Wren; 26 full-day recordings by the itograph, involving 4 incubation periods of 3 females, show that the birds left the nest from 5 to 13 times a day, the median being 8.5 times. Periods on the nest averaged from an hour to nearly 3 hours; periods off from 16 to 22 minutes. There seemed to be considerable variation in incubation rhythm, even in the same bird, from year to year (Hann, 1937; Nice, 1938).

RELATIONSHIP BETWEEN TEMPERATURE AND INCUBATION RHYTHM

As illustrations of relationship between incubation rhythm and temperature, let us examine a number of cases for which sufficient data have been obtained: the Carolina Wren of this study; Laskey's Carolina Wren in comparison with ours; 3 Willow-Warblers, *Phylloscopus*, whose incubations were recorded mechanically (Kuusisto, 1941); 3 Song Sparrows, *Melospiza melodia*, during 4 incubations (92 hours—Nice, 1937:123, Table IX); 5 Song Sparrows, whose incubations (representing 29 days) were recorded mechanically by Baldwin and Kendeigh (Nice, 1937:124); a Barn Swallow, *Hirundo r. rustica*, for which 5 full-day observations were recorded (De Braey, 1946:166 ff.; Nice, 1947); 3 Oven-birds in 4 incubations (covering 26 days), recorded by itograph (Hann, 1937; Nice, 1938).

For all except one of the 17 birds involved in the above studies, the percentage of time spent on the nest decreased with increasing temperature. Thus, our Carolina Wren spent 80 per cent of the daylight hours incubating when the temperature averaged 63.6° F. and 64.5 per cent when it averaged 69° F. In Laskey's study the Carolina Wren spent 63 per cent of the time on the nest at a mean temperature of 78° F., whereas the female of our study incubated 73 per cent of the whole period at a mean temperature of 66° F. The Willow-Warbler (*Phyllo-*

² Courtney Jones (1939. "Rock Wrens at Wupatki," *Southwestern Natl. Monuments, Monthly Repts.*, Suppl. for July, pp. 69-72) found that a Rock Wren [*Salpinctes obsoletus*] averaged 18 minutes on the nest, 15 minutes off. Harold Heath (1920. "The Nesting Habits of the Alaska Wren," *Condor* 22:49-55) observed four nests of the Alaska Winter Wren (*Troglodytes troglodytes alascensis*) and found that periods on the nest ranged from 18 to 21 minutes, periods off, from 2 to 5 minutes.

scopus), incubating during warm weather (with maxima of 80.6° and 82.4° F.) in 1937 spent less time on the nest than did the two females incubating during cool weather (with maxima of 64.4° to 68° F.) in 1938 (Kuusisto, 1941:diagrams 11, 15). One of my Song Sparrows (K7) spent 80 per cent of the time on the nest at a mean temperature of 57° F.; K3 spent 71 per cent of the time on the nest at a mean temperature of 69° F.; and K2 spent 79 per cent at a mean temperature of 55° F., 75 per cent at a mean temperature of 70° F. As temperature increased (48° to 80° F.), there was a consistent decrease (77 per cent to 72 per cent) in the percentage of time Baldwin and Kendeigh's Song Sparrows spent on the nest, with the exception of one bird that incubated 79.5 per cent during an average mean temperature of 75° F. The time spent by the Barn Swallow on the nest shows a consistently descending percentage (74 per cent to 66.5 per cent) with an increase in mean temperature (58.6° to 71° F.). Average temperatures during the Oven-birds' incubation ranged from 59° to 80° F., percentage of time on the nest from 85 and 86 per cent to 73 per cent.

In all cases the length of periods off the nest was correlated with temperature. This was true of our Wren, whose periods off the nest decreased markedly in length during the cool weather of the latter part of incubation (although then another factor may have been involved, namely, increased attachment to the eggs). In the cool weather of 1938, 92 per cent of the Willow-Warblers' absences were very short (less than 10 minutes); in the warm weather of 1937 this was true of only 69 per cent of the absences. The length of periods off the nest of my Song Sparrows averaged 6 minutes (for K7), at a temperature of 57° F., and 8 minutes (for K3), at a temperature of 69° F.; K2 stayed off 7.8 minutes, at an average temperature of 55° F., and 9 minutes, at an average temperature of 70° F. One of Baldwin and Kendeigh's Song Sparrows showed a consistent adjustment to temperature, her periods off the nest increasing regularly from 4.1 minutes, at 43° F., to 7.5 minutes, at 54° F., and all showed a regular *average* increase of periods off the nest, from 5.7 minutes, at 48° F., to 16.5 minutes, at 80° F. The Barn Swallow's periods increased consistently from 2.5 minutes, at 58.6° F., to 5.8 minutes, at 71° F. One Oven-bird (No. 15) stayed off 16 minutes at 59° F. in 1935, and 22 minutes at 63° F. in 1936; the other two averaged 20 minutes at 80° F.

The number of periods off the nest per day decreased with rising temperature, for Baldwin and Kendeigh's Song Sparrows, from 33 to 15; for the Barn Swallow, from 79 to 46; for Oven-bird No. 15, from 9.2 to 5.8. For the Willow-Warblers, periods off the nest were much fewer in 1937 than in 1938 (Kuusisto, 1941:45); Kuusisto gives actual figures for only one nest in 1938 (p. 41); the bird left 27, 27, 30, and 35 + times in one day.

Correlative with the lessening of the number of absences with increasing temperature, is the increase in the length of periods on the nest: for the northern Ohio Song Sparrows a consistent increase from 19.3 minutes to 42.4 minutes; for the Barn Swallow, from 7.2 to 11.9 minutes; for Oven-bird No. 15, from 96 to 170 minutes.

Carolina Wrens and Song Sparrows studied at Columbus, however, decreased the length of periods on the nest with increasing temperature. The Wren of our study averaged 98 minutes on the nest at 64° F. and 71 minutes at 69° F.; Laskey's Wren averaged 57.5 minutes at 78° F.; my Song Sparrows averaged 30.5 minutes at 57° F. (K7), 20 minutes at 69° F. (K3), 30 minutes at 55° F. and 27 minutes at 70° F. (K2).

To summarize: in colder weather the birds increased the percentage of time spent on the nest, shortening the periods off the nest. Ten birds of four passerine species (5 Song Sparrows in northern Ohio, Oven-bird, Barn Swallow, 3 Willow-Warblers) increased the length of periods on the nest, decreasing the number of periods (both on and off). Five birds of two species (3 Song Sparrows in central Ohio and 2 Carolina Wrens) decreased the length of periods (both on and off), increasing the number. It will be noted that in all cases periods off the nest were shorter in cold weather than in warm, while the number of periods (both on and off) differs according to whether the periods on the nest lengthen or shorten.

CARE OF THE YOUNG

Except for giving small notes when fed by her mate, the female Carolina had been quiet in the nest during incubation. On May 12, at 1:43 p.m., she started to chatter, much as she had done when arranging material in the nest, and 16 minutes later she again chattered. The male brought food 6 times between 1:43 and 2:50, when the female left the nest. We then found that the first young had hatched, and there was no sign of the shell. The female had left at 9:54, at which time there were still 5 eggs; she returned at 10:25; unfortunately, no one was watching the nest from 12:40 to 1:15, so we cannot be sure that she did not take a brief vacation, but she may have stayed on continuously for 4 hours and 25 minutes. The male had been feeding his mate 2.2 times an hour on this morning—in contrast to 0.7 times an hour during the previous 81.5 hours of observation, but after 1:46 p.m. he fed his mate 4 times an hour. He showed excitement by loud singing and by flipping his wings. At 5:47 p.m. his mate was absent, and he fed the nestling directly for the first time. The next day 3 more eggs had hatched by 10:00 a.m., and the last one hatched between 12:10 and 4:46.

Two full-day records were obtained: on May 15, when the young were 2 and 3 days old; and on May 22. In addition, we watched from one to 11 hours every day except May 20 while the young were in the nest. A summary of the results is given in Table 3.

TABLE 3
CAROLINA WREN, NORTH LITTLE ROCK, ARKANSAS
CARE OF FIVE YOUNG

| Date (1946) | Hours watched | Feedings | | | | | | Brooding periods (mean lengths) | | Time on nest (%) | Temperature (mean) USWB | | |
|-----------------|------------------|----------|------|----------|------|----------|------|------------------------------------|----------|---------------------|----------------------------|----|-----|
| | | Per hour | | Total | | by ♂ & ♀ | by ♂ | by ♀ | by ♂ & ♀ | | | On | Off |
| | | by ♂ | by ♀ | by ♂ & ♀ | by ♂ | | | | | | | | |
| May 12 | 4* | 6.0 | 0 | 6.0 | 24 | 0 | 24 | 95.7 | 23.7 | 83.6 | 60°F. | | |
| 13 | 4* | 3.5 | 0.5 | 4.0 | 14 | 2 | 16 | 54.0 | 27.7 | 69.3 | 62° | | |
| 14 | 4.5 | 4.2 | 0.2 | 4.4 | 19 | 1 | 20 | 57.2 | 19.5 | 85.2 | 70° | | |
| 15 | 14 | 3.6 | 0.9 | 4.5 | 51 | 12 | 63 | 34.9 | 30.5 | 51.4 | 66° | | |
| 16 | 4 | 3.0 | 2.3 | 5.3 | 12 | 9 | 21 | 17.0 | | 4.7 | 72° | | |
| 17 | 3 | 5.7 | 2.0 | 7.7 | 17 | 6 | 23 | 0 | | 0 | 72° | | |
| 18 | 3 | 5.7 | 2.7 | 8.4 | 18 | 8 | 26 | 0 | | 0 | 70° | | |
| 19 | 3 | 5.0 | 4.0 | 9.0 | 15 | 12 | 27 | 0 | | 0 | 68° | | |
| 21 | 3* | 3.7 | 5.3 | 9.0 | 11 | 16 | 27 | 0 | | 0 | 62° | | |
| 22 | 14.3 | 5.4 | 5.8 | 11.2 | 77 | 83 | 160 | 0 | | 0 | 64° | | |
| 23 | 1 | 6.0 | 8.0 | 14.0 | 6 | 8 | 14 | 0 | | 0 | 70° | | |
| 24 | 11 | 4.0 | 10.1 | 14.1 | 44 | 111 | 155 | 0 | | 0 | 76° | | |
| 25 | 6 | 5.7 | 11.1 | 16.8 | 34 | 67 | 101 | 0 | | 0 | 70° | | |
| 26 | 1 | 7.0 | 11.0 | 18.0 | 7 | 11 | 18 | 0 | | 0 | 66° | | |
| Total period | 77.8 | 4.5 | 4.5 | 9.0 | 352 | 346 | 695 | | | | 67.7° | | |
| First half† | 38.5 | 4.1 | 1.0 | 5.1 | 158 | 38 | 193 | 49.8 | 27.4 | 72.4 | 67.4° | | |
| Second half | 39.3 | 5.0 | 7.8 | 12.8 | 194 | 308 | 502 | 0 | | 0 | 68° | | |

The first young hatched about 1:43 p.m. May 12; 3 more by 10 a.m., and the last by 4:46 p.m., May 13.

Data for 2 all-day records (May 15 and 22) are given in boldface type.

* Watched in afternoon only.

† For brooding: first four days.

For the first 3 days (May 13 to 15) the female behaved much as she had while incubating; she brooded much and fed little. The percentage of daylight hours spent on the nest during these days (72 per cent) was as much as during incubation (73 per cent), and the average length of periods off was much the same (27 minutes now, 31 minutes before). The chief difference lay in the *number of periods off*, which became twice as numerous (12 on the all-day session of May 15, in contrast to 6 and 7 on May 2 and 7), and in the *length of periods on* (50 minutes now, 86 minutes before). (The explanation of the lower percentage of brooding on the cool day of May 13, in comparison with the mild day of May 14, probably lies in the time the observations were made, in the afternoon on May 13, in the morning on May 14; 64 per cent of the morning hours were spent on the nest on May 15, 40 per cent of the afternoon hours.)

The female spent the nights on the nest up to May 18, when the young were 6 and 7 days old; we did not check on this point on May 19 and 20, but on May 21 the female did not come to the nest while we watched from 7:02 to 7:30 p.m., by which time it was very dark. On the following evening, she entered the box at 7:15 p.m., evidently for the night, since she had not left by 7:30. Laskey's female did not brood the young after they were 4 days old despite unseasonably cold weather.

The female showed an almost continuous increase in her rate of feeding, from 0.5 times an hour (on May 13) to 11 times an hour (on May 25). The male had a burst of enthusiasm upon the hatching of the first egg on May 12 and brought food to the nest 6 times an hour, but his rate dropped the next day to 3.5 times an hour, then gradually increased to 5.7 times an hour (on May 17 and 18). On May 21, for the first time, the female outdid her mate; in 18 hours during May 24 to 26 (the last 3 days of nest life) she brought more than twice as many meals as her mate. Omitting the afternoon of May 12, the rate for the *pair* increased consistently from beginning to end, from 4 to 18 times an hour, averaging 9 times an hour for the whole period. When the young were 2 and 3 days old, 63 meals, or 12.6 for each, were brought during the day; when the young were 9 and 10 days old, 160 meals, or 32 per nestling, were brought (assuming that only one bird was fed on each trip, a matter on which we could make no observations). The hourly rate of feeding during the first half of nest life was 5.1, during the last half, 12.8, or two and a half times as high—the same proportional increase as found at 7 Song Sparrow nests (Nice, 1943:231). Beginning with May 16 both parents brought some very large insects.

During the first week our Carolina Wrens showed the same rate (number of trips per hour) in feeding their 5 young as did Laskey's pair in feeding 3 young: 5.1 trips per hour, or one trip per bird for our brood, 1.7 trips per brood for hers. During the last 5 days of nest life,

Laskey's pair made 6.1 trips per hour (only 2 young were then present), whereas our pair, during the last week, averaged 12.8 trips per hour. For the whole period, Laskey's pair averaged 2.2 trips per hour per young, our pair averaged 1.8.

In keeping with the slow pace of the incubation rhythm, both these pairs of Carolina Wrens fed the young rather infrequently. The hourly rates *per brood* of 8 passerine species (Nice, 1943:235) ranged from 39.7 (Great Tits, *Parus major*) to 11.4 (Song Sparrows); 2 other species—American Robins, *Turdus migratorius*, at 6.5, and Oven-birds at 3.7—showed a lower rate than our Wrens. The rates *per nestling* for the 8 species ranged from 8.4 (Wire-tailed Swallows, *Hirundo smithii*) to 3.1 (Song Sparrows); the Robins received 1.7 and 2.1 meals per hour, the Oven-birds 0.8 to 1.2.

The first sac of excreta we saw carried away was one on May 15 (by the male). On May 22 (a full-day observation) the male carried off 12; the female, 16—a total of 28 for the day, or 18 per cent of the number of feedings. During the 11 hours' observation two days later, the male took 4 sacs and the female, 25—again 18 per cent of the number of feeding trips.

LEAVING THE NEST

On May 18 we had first heard notes from the young at some of the feedings. They squeaked when hammering began nearby but not when the basket was touched. The next day they responded with sounds to the shutting of the porch door and to a scratch on the basket. The female now began giving her *tinkle*, denoting mild alarm, at Blue Jays. These *tinkles* were often heard from then on, and the male *churred* more and more vigorously (at times, 70 notes a minute) at the Jays, which never paid the slightest attention. During the last few days, as the female assumed the larger share of the task of feeding the young, the male's role as policeman became more pronounced.

By May 24 the young had become very noisy at meals, and occasionally they gave the location note—*pfitt*. The next day they called at times in response to their father's songs. Between 5:00 and 6:00 p.m. the female fed the young 11 times, the male 3 times, but twice he came to the basket without food and merely looked in.

On May 26, when the young were 13 and 14 days old, the male's first feeding of the day came at 4:48 a.m., the female's at 5:01; both fed the young industriously during the first hour. The young were silent at first, but at 6:09 responded to each of the male's songs with location notes. At 6:43 a nestling was up on the edge of the basket, but promptly hopped back; this performance was repeated at 7:20. The male then came to the basket *without food* 4 times and peered in; once he gave a note, then flew to the west and sang loudly, while the young scrambled about inside the basket. He was apparently *trying to get the young to leave*.

By 7:38 a.m., 4 young Wrens were up on the edge. The female now arrived, scolded, and fed the one young inside; she scolded again, and all disappeared inside. The next minute 3 clambered up again; the female went to the basket without food, hopped in, and all followed her. The male joined them without food, then started to sing from the nearest oak. At 7:42, all 5 young climbed out on the edge, and 2 flew to the shelf under the eaves. The female went into the basket with food, came out, and fed one of the young on top; she then hopped into the basket, giving coaxing notes, and 3 young followed her. The male *churred* in the oak and the female *tinkled*. The male fed a young Wren in the basket and took away a fecal sac. One fledgling flew from the shelf and landed on the floor of the porch. The female went to the basket, then to the young Wren under the eaves, giving coaxing notes, returned to the basket, and fed a young Wren inside. Unlike the male's, her efforts seemed to be *directed toward getting the young back into the nest*.

The bird on the floor called *pfitt pfitt*. With some young in the basket and some fluttering about, the scene became considerably confused. Both parents fed young at 7:53 a.m., the female at 7:59, 8:03, and 8:04. Now it appeared that the female, as well as the male, was trying to lure the young from the nest and its vicinity; she went to the eaves, giving coaxing notes, while the male went into the basket, which then contained only one young Wren. At 8:13 both parents entered the basket, the female carrying an insect; the young Wren followed her out, but the mother did not feed it. All 5 young started to fly about, whereupon we decided to band them. The male scolded vigorously and fluttered to within a few feet of one of us, then left.

We banded 3 young and put them in a trap, and they began to call; the male appeared and *churred*. The fourth fledgling screamed when caught, whereupon the male flew near with slow wing movements—a mild form of “distraction display,” which seems not to have been previously recorded for the Troglodytidae.

The female flew in and out of the porch, giving the “tolling” notes; she returned with an insect, went to the empty basket, then left. Seven minutes later, the male came to the feeding shelf some 15 feet from the young in the trap; the young began to call. The female arrived again with food, going to the empty basket, then hurrying past the trap, calling. The male came 3 times to the basket, looked down at the young in the trap, then left; the female came 4 times, each time hurrying past the trap, calling loudly. At 9:03 she arrived with food, went to the basket, called, alighted on top of the trap, returned to the basket, and left. We then put the trap containing the young under a large drop trap at the side of the house; the male *churred* vigorously, but the female came directly to the young to feed them; we caught and banded her. We released the young at once; they flew some 15 feet and landed well.

The Wrens moved down the hill into the woods, and we did not see the young again. The male returned occasionally, but the female was seen only once—on June 18, when she and the male were examining the nest basket. A pair, apparently juveniles, took possession of the hill. In late July, the male occasionally appeared to chase them with much excited singing, but he was not seen after July 28 although he was watched for until December 18.

EARLY MORNING AND EVENING ACTIVITIES

The beginning and end of activities of both male and female were closely correlated with light. Records for 19 mornings are given in Table 4. The male's awakening songs on 8 clear (one slightly misty) mornings came 27 to 42 minutes (average: 33 minutes) before sunrise; on 2 cloudy mornings, 21 and 27 minutes (average: 24 minutes); and on 2 rainy mornings, 14 and 21 minutes (average: 17.5 minutes). Civil twilight at 35° latitude occurs at 26 to 28 minutes before sunrise at this time of year (Kimball, 1916:617); thus, the first song on clear mornings averaged 6 minutes before civil twilight. The male did not sing as early as the Mockingbird (*Mimus polyglottos*), Robin, Purple Martin (*Progne subis*), Mourning Dove (*Zenaidura macroura*), Cardinal, or the Catbird (*Dumetella carolinensis*), but was always earlier than the Bewick's Wren, Chimney Swift (*Chaetura pelagica*), and Orchard Oriole (*Icterus spurius*).

Three of the male's first visits to the nest on the days the female was laying took place about an hour after his first song, although one (on April 28) must have come about 25 minutes after (see Table 4). During incubation his 4 first visits of the day occurred about half an hour after his first song, whereas 3 first visits to feed the young came at 6, 8, and 18 minutes after. Thus a progressively greater bond to the nest is evident.

The female came to the nest at about sunrise when building and when feeding young. Her very late arrival (7:09 a.m.) on April 24 may have been due to a heavy downpour that began about 2:00 a.m. and lasted well into the morning. During the period of laying, she left the nest from 5 to 8 minutes after sunrise (returning in 23 to 26 minutes to lay). On 3 mornings in the early part of incubation she left the nest 10 to 12 minutes after sunrise; on 2 mornings during the latter half she left 22 to 23 minutes after. We obtained only one record while she was brooding the young: on May 15 she left 29 minutes after sunrise. Here an increasing bond to the nest seems evident after incubation started.

Until May 2 the male roosted in a fold of awning outside a west window of the house; the heavy rain falling that night may have discouraged him from returning. We did not know where he spent his nights after that except for May 25, when we found him once more in the awning. On 5 clear evenings he went to roost from 3 minutes be-

TABLE 4
CAROLINA WREN, NORTH LITTLE ROCK, ARKANSAS
EARLY MORNING ACTIVITIES

| Date (1946) | Sky | Sunrise | Male | | Female | |
|----------------|---------|---------|-------------|------------|--------------|--------------|
| | | | 1st song | To nest | To nest | Left nest |
| Building | Apr. 22 | cloudy | 5:29 | | | |
| | 22 | cloudy | 5:28 | | 5:30 | |
| | 24 | cloudy* | 5:27 | | 5:26 7:09 | |
| Laying | 25 | clear | 5:26 | 4:44 | 5:44 | 5:43 |
| | 26 | clear | 5:25 | 4:50 | 5:58 | |
| | 27 | clear | 5:23 | 4:53 | | 5:33 |
| | 28 | clear | 5:22 | | 5:18 | 5:28† |
| | 29 | cloudy | 5:21 | 4:54 | 6:05 | 5:29 5:26 |
| Incubation | 30 | rainy | 5:20 | 4:59 | | 5:42 |
| | May 1 | misty | 5:19 | 4:50 | 5:24 | 5:31 |
| | | clear | 5:18 | 4:40 | 5:20 | 5:28 |
| | 7 | cloudy | 5:13 | 4:52 | 5:27 | 5:35 |
| | 9 | clear | 5:12 | 4:45 | 5:18 | 5:35 |
| | 10 | cloudy | 5:11 | | | 5:23† |
| Care of yg. | 15 | cloudy | 5:07 | | 5:05 | 5:36 |
| | 19 | rainy | 5:04 | 4:50 | | |
| | 22 | clear | 5:02 | 4:30 | 4:36 | 5:09 |
| | 24 | cloudy | 5:01 | | | 5:07 |
| | 26 | clear | 5:00 | 4:30 | 4:48 | 5:01 |

Time is Central Standard. Hours of sunrise from USWB at Little Rock.

* After heavy rain in latter part of preceding night.

† Called off the nest by male's loud song nearby.

fore sunset to 2 after; on 4 cloudy evenings, from 2 to 13 minutes before sunset; and on 2 rainy evenings, 26 and 28 minutes before. His last feedings of the young usually came around sunset on clear evenings. His last songs were less regular than his roosting or last feeding; only once did we hear him as late as 9 minutes after sunset—on May 23.

While there were eggs in the nest the female always came to the basket before sunset: 1, 2, 5, and 14 minutes before, on clear evenings; 12, 23, and 33 minutes before, on cloudy and rainy evenings. But after the young hatched she always returned after sunset: 4, 5, 7, 15, and 17 minutes after, on clear evenings; 8 and 10 after, on cloudy evenings. In fact, on 3 occasions she had difficulty in finding the basket in the

TABLE 5
CAROLINA WREN, NORTH LITTLE ROCK, ARKANSAS
EVENING ACTIVITIES

| Date (1946) | Sky | Sunset | Male | | | Female | |
|----------------|---------|--------|--------------|-----------------|-------------|------------|-----------------|
| | | | Last song | Last fed yg. | To roost | To nest | Last fed yg. |
| Building | Apr. 20 | cloudy | 6:45 | 6:43 | | 6:43 | |
| | 24 | cloudy | 6:48 | | | 6:44 | |
| | 25 | cloudy | 6:49 | | | 6:45 | 6:26 |
| | 26 | clear | 6:50 | | | 6:52 | 6:49 |
| | 27 | clear | 6:50 | 6:48 | | 6:52 | 6:45 |
| | 28 | clear | 6:51 | | | 6:53 | |
| | 29 | rainy | 6:52 | | | 6:26 | |
| Incubation | May 30 | cloudy | 6:53 | 6:33 | | 6:40 | 6:20 |
| | 1 | clear | 6:53 | 6:47 | | 6:50 | |
| | 2 | rainy | 6:54 | 6:24 | | 6:26 | 6:42 |
| | 5 | clear | 6:57 | 6:49 | | | 6:43 |
| | 7 | clear | 6:58 | 6:53 | | | 6:56 |
| Care of yg. | 12 | clear | 7:02 | | 6:55 | | 7:09 |
| | 13 | cloudy | 7:03 | 7:02 | | | 7:13 |
| | 14 | clear | 7:04 | | | | 7:08 |
| | 15 | cloudy | 7:04 | | 6:49 | | 7:12 |
| | 16 | clear | 7:05 | | 7:05 | | |
| | 17 | clear | 7:06 | 7:08 | 7:07 | | 7:23 |
| | 18 | clear | 7:07 | 7:08 | 7:07 | | 7:22 |
| | 19 | cloudy | 7:08 | 7:02 | | | |
| | 21 | clear | 7:09 | 7:12 | 7:07 | | |
| | 22 | clear | 7:10 | | 6:43 | | 7:15 |
| | 23 | clear | 7:10 | 7:19 | 7:14 | | 6:59 |
| | 25 | clear | 7:12 | 7:14 | | 7:15 | 7:14 |

Time is Central Standard. Hours of sunset from USWB, Little Rock.

dark, having to alight on the stepladder below the nest on May 15, "stumbling about" on May 17, and on May 13 she could not find the nest on her return at 7:13 and went away. We turned on the light in our part of the porch. She came back at 7:16, scolding vigorously, flew to the ladder, made an unsuccessful attempt to reach the nest, and with the second try succeeded.

On the 5 days for which we have records of his last feedings and her final return to the nest, his feedings averaged 8 minutes before sunset; her returns, 8 minutes after. His day started earlier and ended earlier than hers. Evening activities for 24 days are shown in Table 5.

SUMMARY

A nesting at North Little Rock, Arkansas, of a color-banded six-year-old male Carolina Wren, *Thryothorus ludovicianus*, mated with an unbanded mate, was watched some 250 hours, from the arrival of the female on April 19, 1946, to the leaving of the 5 young on May 26.

On April 20 the pair built sporadically in a tool-shed and in a basket on the sleeping porch; on April 21 they built most of the nest in the latter place between 8:00 and 10:00 a.m., the male bringing 205 loads, his mate 104. After that, his zeal diminished; in a total of 2 hours and 30 minutes of observation during the rest of the day he brought 30 loads, she 49. He brought no more material after that, but she carried in lining for 4 more mornings and continued to bring hair or grass blades occasionally until May 6, the eighth day of incubation.

Five eggs were laid, starting April 25, the female spending the night in the basket from that date. She left the nest 5 to 8 minutes after sunrise, returning in 23 to 26 minutes, and stayed on to lay from 30 to 64 minutes.

Incubation lasted 14 days and was performed entirely by the female. During 92 hours of observation she incubated 73 per cent of the time, staying on the nest from 31 to 174 minutes, averaging 86 minutes, and staying off the nest from 8 to 84 minutes, averaging 31. Two all-day observations gave the following results: fourth day, 5 periods on—averaging 103 minutes, 6 periods off—averaging 46.5 minutes; ninth day, 6 periods on—averaging 106 minutes, 7 periods off—averaging 24 minutes. The mean temperature of the first day was 8° F. above normal; on the second, 4° below normal. During the first 5 days, 64.5 per cent of the time was spent on the nest, with a mean temperature of 69° F.; periods on the nest averaged 71 minutes and periods off, 39 minutes. During the last 9 days, 80 per cent of the time was spent on the nest, with a mean temperature of 63.6° F.; periods on the nest averaged 99.6 minutes, periods off, 24.4 minutes.

Periods on and off the nest (as also with 2 Carolina Wrens observed by Laskey) were very much longer than those of most passerines so far studied. Females of 11 species left the nest 11 to 90 times a day—in contrast to the 6 and 7 times of the Carolina Wren of this study; the Oven-bird is the only passerine known to have an at all comparable rhythm.

In 7 studies of incubation in passerines it was found that the colder the weather, the more time spent on the nest and the shorter the absences of the parent. In some cases the absences were also more frequent, the periods on the nest shorter than in warm weather; in other instances periods on the nest were longer.

The male Carolina Wren fed his mate to some extent during nest building, egg laying, and incubation—93 times in the 92 hours of the incubation period.

The young hatched on May 12.

The nest was watched 77.8 hours during the nestling period, including 2 all-day sessions; when the young were 2 and 3 days old, the male made 51 trips, the female 12—together making 12.6 trips per young; when the young were 9 and 10 days old, the male made 77 trips, the female 83—32 trips per young. During the first week the parents together averaged 5.1 trips per hour; during the last, 12.8. The male increased his rate from 3.5 an hour to 7, the female from 0.5 to 11; the average of each for the whole period was 4.5. Excreta were carried off after 18 per cent of the feedings on May 22 and 24 (14 and 11 hours observation).

The young left at 13 and 14 days. After vigorous feeding during the first hour of May 26, the male began to lure the young out of the nest by visits without food and by loud singing nearby; the female, on the contrary, 3 times got the young back into the nest basket after they had left it. By 8:00 a.m. the female started luring the young out with coaxing notes and by refusing to deliver the food she carried.

When we caught a fledgling and it screamed, the male showed a mild form of distraction display; this is apparently the first record of this behavior in the Troglodytidae.

Activities of both male and female were closely correlated with light. The male's awakening song on clear mornings averaged 6 minutes before civil twilight. The female came to the nest about sunrise when nest building and feeding young; she left the nest, when laying, 7 to 8 minutes after sunrise. The male's day ended at about sunset except on 2 rainy evenings when he came to roost 26 and 28 minutes before sunset. The female behaved in much the same way while there were eggs in the nest, but after the young hatched her return to the nest was later, once 17 minutes after sunset; on 3 occasions she had difficulty in finding the nest in the dark.

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5725 HARPER AVENUE, CHICAGO 37, ILLINOIS
NORTH LITTLE ROCK, ARKANSAS